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THE MARINE IGUANA OF THE GALÁPAGOS ISLANDS, ITS BEHAVIOR AND ECOLOGY

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Introduction

A large lizard which lives on lava reefs at the edge of the ocean, feeds on seaweeds at depths up to 35 feet, basks in huge aggregations, and has communal nesting grounds on a remote archipelago of the Pacific Ocean, is indeed a unique wonder of evolution.

Such a lizard is the marine iguana (*Amblyrhynchus cristatus*) which is endemic to the Galápagos Islands, an archipelago of approximately 25,000 square miles lying 600 to 700 miles west of Ecuador in equatorial waters.

It belongs to a large family of lizards, the Iguanidae, which ranges primarily throughout the New World. Two other genera of this family are also found on these islands; the large land iguanas (*Conolophus*) which are also endemic, and the lava lizards (*Tropidurus*) which are also represented on the continent of South America.

This account concerns the marine iguana, which was studied in particular to relate its behavior patterns and ecological requirements to other genera and species of the family.

The marine iguana was observed by this writer on two expeditions to the Galápagos Islands. The first, with the support of a grant from the National Science Foundation (G-19420) extended from late January to early June of 1962. The second, as an invited scientist participant with the Galápagos International Scientific Project, supported by the National Science Foundation grant GE-2370 to the University of California, included five weeks on these islands. The California Academy of Sciences was a co-sponsor of the latter project.

The base of operations for these expeditions was the Charles Darwin Research Station, located near the village of Academy Bay on the southeast corner of Indefatigable Island, the central island of the archipelago. This research station is maintained by the Charles Darwin Foundation for the Galápagos Islands which is international in scope.

The marine iguana was described by Bell in 1825. Garman (1892) mentions that there appeared to be three forms of this species. Today seven races are recognized (Eibl-Eibesfeldt, 1962) though these descriptions fail to include those marine iguanas found on such islands as Bindloe and Wenman. The seven described races and the islands where they are found are: *Amblyrhynchus cristatus cristatus* Bell—Narborough; *Amblyrhynchus cristatus hassi* Eibl-Eibesfeldt—Indefatigable; *Amblyrhynchus cristatus albemarlensis* Eibl-Eibesfeldt—Albemarle; *Amblyrhynchus cristatus venustissimus* Eibl-Eibesfeldt—Hood; *Amblyrhynchus cristatus mertensi* Eibl-Eibesfeldt—James and Chatham; *Amblyrhynchus cristatus sielmanni* Eibl-Eibesfeldt—Abingdon; *Amblyrhynchus cristatus nannus* Garman—Tower.

The geographical range of the marine iguana includes the coastal areas of all of the islands, islets, and sea rocks of the archipelago.

Population Distribution

No complete survey of the abundance and distribution of the marine iguana throughout the archipelago has been undertaken and this is probably not feasible because of the nature of the coast lines. From my own observations and from literature sources, these lizards occur in certain large concentrations with many sparse populations scattered around the island coast lines.

The large aggregations observed were associated with areas of lava reef that offered feeding sites and which had associated land areas with suitable nesting conditions.

The largest populations of marine iguanas were observed at Punta Espinosa on the northwest corner of Narborough Island and at Punta Suarez at the west end of Hood Island. Other large populations were noted on Jensen Island lying in Academy Bay off the southeastern coast of Indefatigable Island, the southern shores of Bindloe and Abingdon islands, and the coasts of Indefatigable Island in the area of Academy Bay.

Small numbers were recorded on Wenman Island, near Punta Vincente on northwestern Albemarle Island, at James Bay on James Island, and at Tortuga Bay on Indefatigable Island a few miles west of Academy Bay.

These lizards were very scarce, only one or two to a few individuals being seen along the area of Post Office Bay and Black Beach on Charles Island and on the north side of Duncan Island. At Punta Ceravallo at the eastern end of Hood Island, Gardner Island near Hood Island, and on Barrington Island,

small scattered populations were present. None were observed near Wreck Bay on Chatham Island.

Slevin (1935) cites references to a large population of marine iguanas at Iguana Cove, Albemarle Island.

The observations included in this paper concern primarily the large populations located at Punta Espinosa on Narborough Island, Punta Suarez on Hood Island, and those in the vicinity of Academy Bay.

Punta Suarez forms the western tip of Hood Island. The north side of the point is formed of intermittent coral-sand beaches between low lava exposures. The tip of the point is an array of huge lava boulders which extend back east along the south side. The land rises from north to south forming cliffs reaching in some places to 50 feet. Below the cliffs are exposed reefs and boulder beaches of lava which vary in expanse with the tides. The land also rises from west to east, reaching a plateau strewn with rough lava outcrops and boulders. The lower areas are a tangle of bushes while the higher areas are more open with some patches of soil supporting sparse grass cover. This latter area is the nesting ground for the waved albatross and blue-footed booby. Along the cliff edge are the nests of the masked booby and the swallow-tailed gull. Galápagos doves, mocking birds, and geospizid finches are common, and the short-eared owl is present here as a predator. Sea lions frequent all of these shores.

Punta Espinosa projects from the northeast corner of Narborough Island (Fernandina Island) into the cool waters of Bolivar Channel.

There are two beaches on the approximately quarter of mile of lava spit which forms Punta Espinosa. The proximal portion of this point is covered by a white beach composed of a mixture of coral and lava sand with many small weathered and fragmented shells and other invertebrate remains mixed in. This beach overlies lava, covering an irregular area about an acre in size. Another similar but smaller sandy area is near the end of the point. To the south of this point is a well protected lagoon, with the open ocean to the north. The base of the point and edges of the lagoon are covered by thickets of mangroves. Intermittent lava exposures and small lagoons and beaches extend for a mile to the northwest of the point. Away from the point inland, extensive fields of bare lava are encountered but a few yards from the sea.

Perhaps the most concentrated biomass of lizards per unit of area exists on Punta Espinosa, and without doubt, at high tide the rock (steep rising lava fault) at the tip of the point has the largest lizard biomass anywhere in the world today. At such times, nearly every square foot is occupied by one or more marine iguanas.

Three estimates (in 1964) of the number of lizards on this rock, concentrated in an area of approximately 60 by 20 feet, were 350, 300, and 500 on January 25 (1:30 P.M.), 26 (8:00 A.M.) and 27 (2:15 P.M.) respectively.

A census of the entire point on January 25 gave 1,558 lizards and similarly 1,885 on the 27th. These lizards were not scattered at random, but were, for the most part, in aggregations on the reefs within 30 feet or less of the water.

A rough estimate of the biomass for the point rock, with 500 individuals averaging 76 cm. in total length and 3 pounds 8 ounces in weight would be 1,750 pounds.

Jensen Island is the small island lying in Academy Bay (area approximately 5 acres). A census of this island on April 6, 1962, yielded approximately 1,800 individuals, primarily in aggregations of from 30 to 200 on the reef fringing the island. Dowling (1962) estimated 2,000 iguanas on this island.

Juveniles were not as apparent in the reef aggregations and apparently the ratio of juveniles to adults is less than 1 to 10. Juvenile aggregations of as many as 12 were observed, these small aggregations being separate from adult aggregations. Juveniles were interspersed in many large aggregations however.

Slevin (1935) states that some large males reach a length of 5 feet and a weight of 20 to 22 pounds. From my experience, these individuals would be very exceptional on the islands today.

At Academy Bay in 1962, 64 males ranged from 15.1 (snout-vent length) 35.5 (total length) cm. to 49.0/114.0 cm. in length (average 31.8/74.8 cm.) and in weight from 4 ounces to 10 pounds 10 ounces (average of 3 pounds 2 ounces). The 46 females recorded for size ranged from 14.4/33.0 cm. to 33.2/78.5 cm. in length (average of 25.4/59.4 cm.) and in weight from 3 ounces to 3 pounds 4 ounces (average of 1 pound 7 ounces) (fig. 1).

In late January, 1964, at Punta Espinosa on Narborough Island, 21 males ranged from 19.0/44.5 cm. to 43.0/107.0 cm. (average 34.1/81.8 cm.) in length and from 10 ounces to 5 pounds 11 ounces (average of 4 pounds 6 ounces) in weight, while 5 adult females ranged from 26.0/58.0 cm. to 35.0/88.0 cm. (average of 29.0/70.1 cm.) in length and from 1 pound 4 ounces to 4 pounds 4 ounces (average 2 pounds 3 ounces) in weight.

The 12 territory holding males at Punta Suarez on Hood Island captured in early February, 1964, ranged from 33.5/84.0 to 40.0/93.5 cm. (average 36.1/88.9 cm.) in length and from 3 pounds 6 ounces to 6 pounds 8 ounces (average of 4 pounds 7 ounces) in weight. These included the largest males observed in this area.

Beebe (1924) recorded individuals of 35 and 41 inches, the latter weighing 13 pounds.

PERIODICITY

All recorded observations on the marine iguana have been of short duration, very few of more than a few weeks, thus the annual life cycle of activities must be deduced from scattered evidence.

My observations indicate that these cycles may vary by as much as a month between populations on the eastern and western ends of the archipelago, the western populations breeding first.

The breeding season starts in December on Narborough Island and about one month later on Hood Island which lies in the southeastern section of the archipelago, as evidenced by territorial behavior of the males and nesting activity of the females. The territorial behavior and breeding begin to wane by the end of January on Narborough and it was absent on Hood Island early in April of 1962. The egg-laying period follows closely on the breakdown of territories, commencing in late January or early February on Narborough Island, with some laying still in evidence on Hood Island in mid-April. The egg-laying period probably extends over a period of 3 to 4 weeks.

When the females are on the nesting beaches, the males are again forming aggregations and are joined by the females as they complete their egg laying. These aggregations are apparent until late in the year when territoriality again begins to appear in the males.

The hatchlings begin to emerge in May, and on Hood Island, I would predict they would emerge as late as early July.

The garúa season, a period when a damp heavy mist hangs over these islands, extends from June into October. It appears that the annual cycle of the marine iguana is adapted to avoiding this cooler period for its reproductive activity, the periods of greatest activity being between December and May.

Except for nesting females, I noticed no nocturnal activity by marine iguanas. Since this equatorial area has little variance in sunrise and sunset, there is little change in the daily cycle of activities. Perhaps the greatest influences on the daily cycle are the temperature and the tides.

From my observations, there did not appear to be any significant difference in daily movements to and from the feeding reefs between the breeding and non-breeding season. Males preoccupied with territoriality leave their territories to go to the reef to feed, but they did not feed every day.

The marine iguanas spend the first hour or two after sunrise (6:00 to 6:15 A.M.) basking in the morning sun, with many beginning to move to the reefs or into the sea between 7:30 and 8:00 A.M. Many remain on the reef and do not feed. If the tide is low, many of those feeding remain on the reef and bask during the late morning and into early afternoon.

If the tide is high during the morning, some go out to sea to feed, while others, but fewer numbers, may feed on the reefs in the rolling and crashing incoming tide. If the tide is low during the afternoon, there are some iguanas, but fewer in number, feeding and basking on the reefs.

Activity slows down between noon and late afternoon, with a very slight increase in the later afternoon. During hot afternoons many iguanas seek the shade of reef crevices, large boulders, and mangroves (if nearby) but still

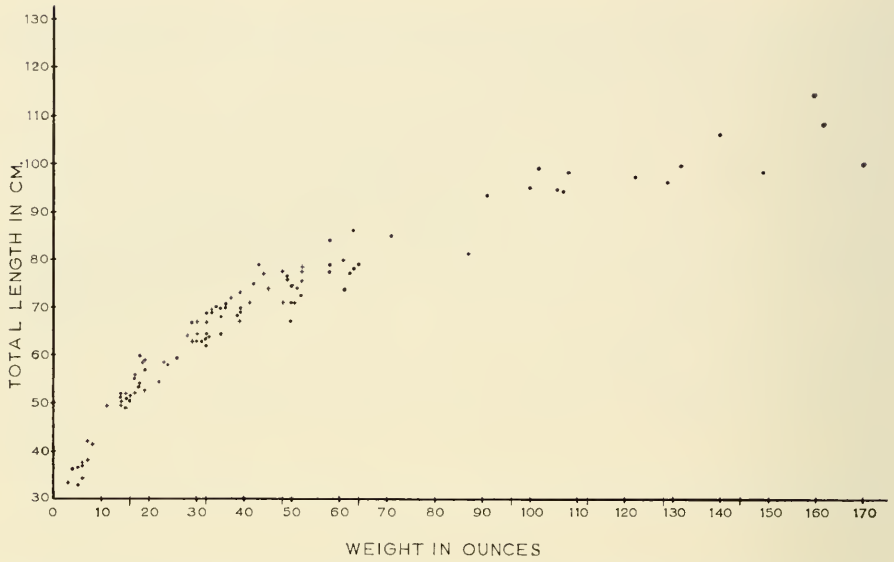

Figure 1. Scatter diagram indicating weight-length relationships of marine iguanas recorded near the Charles Darwin Research Station, Academy Bay, Indefatigable Island, in 1962. ● Male, + female.

there are many on such occasions that continue to bask on the reefs in full exposure to the hot overhead sun.

Just before sunset (6:00 to 6:15 P.M.) many retreat into crevices or beneath boulders, but others spend the night exposed on the reef. They sleep in these positions, those in the crevices hanging on the perpendicular sides or resting on ledges with their heads on the lava. On islands where they live on reefs backed by thickets of vegetation, many retreat into these thickets at night and also use these for shade retreats during the afternoon heat. They readily climb the stout branches of this vegetation.

The temperature relationships of the marine iguana are undoubtedly complex and unique. This lizard basks or spends most of the daylight hours exposed to the direct rays of the overhead sun, lying on the hot black lava, and moves to the spray zone, edge of the reef, or into deep water to feed. This deeper water (20 to 30 feet deep) is much cooler than the reef temperatures, and well below the temperatures maintained by the lizards out of water.

A series of ambient temperatures taken on February 26, 1962, at Punta Espinosa on Narborough Island are as follows (taken near midday).

In sun—1.5 m (in wind)	27.7°C.
Sand surface—in sun	48.8°C.
Lava surface—in sun	40.5°C.

In shadow of crack in lava	33.5°C.
Water (sea) at 10 cm.	28.8°C.
Water (sea) at 50 cm.	27.2°C.
In nest burrow	30.3°C.
Sand in shadow	43.3°C.
Deep crevice in lava (10 feet)	31.5°C.

The cloacal temperatures of 14 adult marine iguanas in this area ranged from 30.5°C. to 36.8°C. (average 34.1°C.). The cloacal temperature of about 34°C. appears to be their optimum, for two other series of cloacal temperatures taken on other islands agree very closely with this. The cloacal temperatures for 129 iguanas at Academy Bay on Indefatigable Island in 1962 ranged from 28.2°C to 40.0°C. (average of 34.15°C.). A series of 38 cloacal temperatures taken on Punta Suarez on Hood Island on April 16, 1962, ranged from 30.0°C. to 37.7°C. (average of 34.26°C.). These cloacal temperatures were taken throughout the daylight hours and show no significant differences during the day. How much the cloacal temperature is affected when the iguana goes to the sea to feed needs to be investigated, and though it undoubtedly drops, the lizard is still active in this cool water and is able to remain below water for 15 to 20 minutes at least, and to feed actively.

Feeding Behavior

The marine iguana is a herbivore and is adapted morphologically, physiologically, and behaviorally to living at the edge of the sea, feeding in the sea, and resting and reproducing on the lava reefs next to the water.

The apparent reason why this lizard enters the water is that it does so to feed; sometimes perhaps, it uses the water route for moving from one area to another. Therefore, it can be assumed that certain of its physical characteristics are adaptations contributing to its herbivorous habit.

The iguana body is elongate and fusiform. The tail is compressed into a propelling structure which efficiently moves this lizard along the surface or beneath the surface of the water. The long, sharp, recurved claws permit the lizard to hold fast to the lava in heavy seas or when submerged in deep water. The snout of the iguana is short and blunt and this enables it to get its jaws into close contact with the substrate, especially the side of the head. The tricuspate teeth are flattened laterally and lie in single rows along the sides of the jaws immediately inside of the labial scales. In this position they provide an effective serrated surface to rasp short-growing algae from the submerged and exposed reef, or for browsing on more luxuriant algae in deeper waters.

At low tide at both Punta Espinosa and Punta Suarez, certain exposed reefs were often covered by numerous grazing marine iguanas. There was no apparent coordination in these feeding efforts, each lizard moving about independently of the actions of others.

When feeding, the iguana turns its head sideways, brings the jaws across the lava in a rasping and tearing type of movement, and with a twist of the head it jerks away, cropping off the algae. While doing this it holds tightly to the lava, for the surf frequently crashes over the reef, at times completely submerging the feeding lizard. I never saw one dislodged by the force of the surf.

The feeding iguana slowly works its way forward, about one to two inches at a time, over the reef, rasping or tearing a few times, raising its head to swallow or to rest (up to a couple of minutes). In this manner it may move over 15 to 20 feet of the reef, moving in an irregular pattern, probably determined by the presence of the food. This sequence of intermittent feeding and resting may last up to a half hour, after which the lizard moves out of the reach of the surf, and flattens and basks, or moves away from the reef to a location above the tide line.

When feeding in a tide pool on the reef, the pattern is the same for the submerged lizard. One was recorded as remaining submerged for 4 minutes while feeding and slowly moving over the bottom of the tide pool 4 to 10 inches below the surface.

Along the reef-studded coast of many islands, I was often struck by the presence of marine iguanas in deep water. Many of these lizards were not swimming towards any particular mark, but appeared to be freely floating on the ocean surface, bobbing like corks.

At Punta Espinosa in 1962, and again in 1964, large numbers of iguanas were seen at sea, as many as 50 heads seen from one view. Some of these were at least 450 yards from the nearest exposed reef. On February 1, 1964, while on a trip in a small skiff to an area five miles west of this point, we encountered many marine iguanas swimming far from shore. Three days later, on a boat trip one to two miles south, we also encountered many iguanas in deep water, 600 to 700 feet from the nearest shore. All of these lizards were of adult size.

When approached, within variable distances of a few feet up to 50 feet, a floating iguana quickly dived and usually was not seen again.

Darwin (1835) suspected the deep-water feeding habit of these lizards when he wrote his diary: "I have reason to believe it (seaweed) grows at the bottom of the sea, at some little distance from the coast. If such be the case, the object of these animals occasionally going out to sea is explained."

Off the north side of Punta Espinosa, a reef lay approximately 100 feet off shore. This reef was only slightly exposed at the lowest tide. At mid-morning of February 28, I watched this area for two hours. During this time, I saw iguanas appear above the reef, where no lizards had been seen for at least five minutes, others were seen swimming to this area and disappearing (diving), another was out to sea 200 feet beyond the reef; at times lizards appeared at the surface (one timed at two minutes) where they floated, then

dived again, while others surfaced in this area and swam to my observation reef. All of this activity indicated that they probably were diving to feed along this submerged reef. Similar observations were repeated the next day.

One of the skin divers of our party, Mr. Ted Hobson, reported at first seeing these iguanas feeding down to six feet under the water on the abundant seaweed. He also reported seeing them surface with large pieces of seaweed hanging from their mouths.

On the above-mentioned trip to the south of our camp, I took along a face mask and proceeded to watch these lizards under water. The iguanas were widely dispersed so that no more than two were ever seen at one time beneath the surface. They were down to depths of 20 feet, swimming or resting on the large lava boulders which formed the bottom. Small sharks and schools of groupers and other large fish swam close by, but the iguanas showed no response to them. Though they appeared to hang on with the claws when resting, I observed one which appeared able to control its buoyancy, for it seemed to float freely at this depth (15 feet). When they swam, they folded back their legs and propelled themselves by undulating the tail, moving over the bottom and under ledges with ease. When stopped on the bottom, they intermittently grazed on the seaweed.

I observed one continuously for three minutes. During this time, it blew some bubbles from its nostrils. I assume this lizard had already been down for at least a minute or two, and when it swam away it showed no indication of surfacing. I estimate that some marine iguanas may stay submerged for as long as 15 to 20 minutes. With only a face mask, I found it difficult to keep track of individual iguanas for very long as they moved about in deep water. This was made more difficult because of the cool temperature of the water (23°C.), which chilled me in 15 to 20 minutes. That the marine iguana, a poikilotherm, is able to be active and feed at this cool temperature, is another wonder of its unique physiology.

Hobson (1965), with the aid of a depth gauge, later recorded marine iguanas feeding down to depths of 35 feet and reports on other underwater observations and shows a photograph of a marine iguana swimming in deep water. He reports on an iguana staying submerged for over 30 minutes.

Darwin (1835) reports that a seaman aboard the H.M.S. *Beagle* sank a marine iguana with a heavy weight attached to it, in an attempt to kill it, but when the lizard was drawn up an hour afterwards, the lizard was quite active.

Most of the feeding observed took place during the low tides, and particularly when these occurred during the morning hours. There was a general movement to the exposed reefs in mid-morning. However, the presence of many iguanas at sea during high tide indicates that they also feed at this time. Most swimming lizards were observed during morning hours.

On March 1, 1962, at Punta Espinosa, an adult iguana was observed feeding far back in a shaded, calm, shallow mangrove pool. The lizard worked back and forth, entirely under water, propelling itself with its tail. It moved from the base of one mangrove to that of another, grasping and tearing algae from the base of the mangrove trunks. This alga was one to two inches in length and was identified by Dr. Yale Dawson as *Bostrychia* sp.

Small groups of juveniles were seen feeding in the spray zone of the reef, separated from the adults.

During February, 1964, stomach and intestinal contents were obtained from four adult iguanas (two each from Hood Island and Jensen Island). The physical state of these contents varied from amorphous masses of partially digested algae to large fragments of broad filamentous algae, some pieces measuring as long at three inches. The following identifications of the algae were made by Dr. Paul C. Silva, Senior Herbarium Botanist, University of California, Berkeley.

The Hood Island iguanas had eaten *Tylotus ecuadoreanus* Taylor, *Bryopsis indica triscriata* Dawson, *Plocamium pacificum* Kylin, *Prionitis abbreviata* Setchell and Gardner, *Glossophora galapagensis* Farlow, *Lophosiphonia villum* (J. Agardh) Setchell and Gardner, and *Pterosiphonia paucicorticata* Dawson. The Jensen Island iguanas had eaten *Blossevillea galapagensis* (Piccone and Grunow) Taylor, *Prionitis abbreviata* Setchell and Gardner, *Gelidium hancockii* Taylor.

All stomachs contained bryozoans, and one Hood Island lizard had fragments of small crabs present, while another had shrimp remains.

A more thorough study might indicate that there is some selection of algae, for there were algal species present which did not appear in the stomachs (Silva—personal communication). However, the above data indicate that a broad spectrum of algae are eaten (10 genera represented).

One late afternoon, on the reef at Punta Espinosa, a marine iguana was observed eating the dried feces of its own species.

It was not uncommon to see one of these iguanas protrude its tongue into contact with the substrate, doing this intermittently as it moved to a new area of the reef. It appeared to be testing, perhaps for a familiar taste. This suggests that, at times, a particular male may be able to recognize the previous presence of other males in this manner, or that feces may be used in sign posting. This possibility should be investigated further.

On May 6, 1962, while visiting with the Karl Angermeyers at Academy Bay on Santa Cruz Island, Karl demonstrated his interesting relationship with the marine iguanas which lived on the lava reefs adjacent to his home, which was built on a lava ledge at the edge of the water. These iguanas wandered back and forth over his porch and even into his living room. Though hesitant to be touched, they would walk close to a person and to the Angermeyers' large

dog. Karl stated that he often was able to call the iguanas to the porch to be fed. He then proceeded to feed these herbivorous animals. He placed a dish of pieces of raw goat meat on the porch. First one iguana, and then as many as five were moving quickly up to the dish to snatch a piece of meat and quickly gulp it down. Karl stated they would eat oatmeal and other foods, and that he had seen them catch cockroaches in his living room. I took motion pictures of the iguanas feeding on the goat meat. A picture of Karl feeding an iguana by hand in the presence of his dog and cat can be seen in Angermeyer, 1963.

Movement

On January 27, 1964, a series of 14 males were captured on one of the lava exposures (Cactus Rock) on the northwest base of Punta Espinosa. These males were selected because they were thought to show slight territorial tendencies; they were on prominences and separate from aggregations at the time captured. They were also the largest males observed in this area during the morning period when captured. Each was given a different number (painted on the side) and a record of its position when captured and released recorded (the same).

During the evening of January 28, in the dark with the aid of a flashlight, 26 individuals were given prominent yellow marks with a can of spray paint while they were sleeping or resting on the reef and in a crevice in one restricted area of Cactus Rock. These lizards were not handled, so no record of size or sex was obtained, but it is thought that most were adult females.

On January 29, a series of 12 marine iguanas were captured on Cactus Rock. Each was painted with a large letter X plus a number. Numbers 1 through 6 were then taken to an area on the shore one-quarter of a mile northwest of Cactus Rock and released; numbers 7 through 12 were released approximately one-quarter of a mile east of Cactus Rock, near the end of Punta Espinosa.

With the exception of one morning, the position of these iguanas was checked for at least twice each day through February 4.

Four of the six X-series iguanas released one-quarter mile northwest were seen again. One of these had moved further away from Cactus Rock when seen on February 3. Another appeared back on Cactus Rock on February 1 and on the 2nd had returned back northwest to the area where released. The other two returned to Cactus Rock (one on Jaunary 31; the other on February 1) where they remained, moving about this study area.

All six of the X-series released one-quarter mile east at the point area were subsequently observed back at Cactus Rock; three on January 30, one more on February 1, another on the 2nd, and the other on the 4th. Five of the six were still on the study area on the last day of observations.

Because of the nature of the lava reefs and beaches and because of the large size of the marine iguanas, I feel that there was only a slight possibility of not seeing a marked individual were it present on Punta Espinosa. The observer walked slowly along noting all lizards and examining all crevices in the lava. These lizards were approached to within six feet or less before they fled, and then they only moved a short distance of a foot or two to a few yards.

The 14 males released on January 27 showed quite variable degrees of movement.

Three individuals were seen only the first two days after release. One of these had moved to a reef to feed, at low tide, before disappearing.

Three were observed only for the first three days after release. During these three days the maximum distance separating them was 60 feet.

Two were seen only for the first five days following release, one always within 10 feet of its original capture point, the other 60 feet away, except on the last day of observations when it had left the area and was approximately one mile northeast along the coast.

Two disappeared after six days. One of these was always within 60 feet of its point of original capture, except when observed over a submerged reef about 100 feet out at sea. The other moved back and forth over an area of 100 feet along the shore and on the sixth day had moved to another lava exposure about 150 feet away.

One was on Cactus Rock, within a 50-foot area, for seven days and when last observed on the eighth day was approximately one mile to the northwest along the coast.

Three were recorded over the nine days of observation. One was seen the first two days, was gone for two days, and was next observed off Cactus Rock, one-quarter of a mile east, where it remained through the ninth day. Another left the area and moved to a beach three-eighths of a mile east for two days and then returned to Cactus Rock, remaining within 15 feet of the point where originally observed. The other, not seen on the seventh day, was otherwise always seen within 35 feet of its original point of capture, usually in a crevice in the lava.

Of the 26 lizards marked during the evening of January 28, only 12 were seen the next morning; 7 were still in the same area, one had moved 60 feet, 3 had moved off the area and onto an exposed reef 150 feet away. Seven only were seen on the study area on January 29. By the next afternoon, 9 were on the area, while 2 more were seen in the large aggregation at the end of the point about 2,000 feet east. During January 31, 12 were on the study area, randomly dispersed, while another was out at the point where 3 were seen the day before. On February 1, 8 were in the area where they were marked, 3 more were on the study area, one was at the point, one was 200 feet off the

area, and one was on the nesting beach 200 feet south. Eleven were on the study area and one off the area on February 2; only 7 were on the area and two off area on the 3rd. The last day of observations was February 4 when 7 were on the study area, 4 of these in the original marking area.

On February 13, 1964, a series of 12 males in breeding coloration were captured and given painted numbers, at Blow Hole Cliffs (my designation) on the south side of Punta Suarez, Hood Island. These were all of the males spaced at intervals along 200 feet of cliff rim and each was thought to be defending a territory. The movements of these lizards were recorded by noting their positions at least twice a day, through February 19.

All but one individual were observed throughout the entire period, and this one was not seen only on the last two days.

Eight were observed to move from their cliff-rim territory to the reef (exposed at low tide) and back at least once, and four of these more than once.

Three were observed only on the cliff rim or above the cliff, while two others were observed below the cliff only once, being on or near their respective territories at other times.

The others showed daily movement between the cliff area and the boulder beach or reef.

The greatest distance between any two points of observation for any lizard was 180 feet, most distances being under 100 feet, while two were always within 10 feet or less of their original point of capture (for seven days).

The pattern of movement of marine iguanas at Cactus Rock for the period of time of this study, indicated a tendency for most lizards to be more closely associated with Cactus Rock than with any other area, but showed no limited or territorial confinement, with random movement over the study area, perhaps spending two or three days in a restricted area, and infrequent movements to other parts of Punta Espinosa. Homing tendency was strongly indicated when removed from the area.

The 14 males marked at Blow Hole Cliffs showed much more restricted movement than those at Cactus Rock, and they also followed a more definite pattern in their daily activity. The frequent display activity and defense of a restricted area indicated that these males were still territorial. When they moved from their territories, it was usually to the reef to feed or bask on the boulder beach, after which most were seen back in their territories. Thus the territorial activity appeared to restrict movement at Blow Hole Cliffs in contrast to general wandering found at Cactus Rock.

In comparing the movements of the marked marine iguanas at Cactus Rock (Punta Espinosa) and Blow Hole Cliffs (Punta Suarez), it is important to remember that territoriality was practically lacking at the former and much in evidence at the latter.

The marked males at Cactus Rock showed no particular patterns of movement, rather, some moved away shortly and were not seen again, others went away and returned, and only one gave any strong indication of restricting his movements to a limited area, a possible territory. These records do indicate, I believe, that these lizards were familiar with the Punta Espinosa area and spent most of their time at Cactus Rock.

The movements of the 26 yellow-marked individuals were similar to those of the above males. Though a few were observed every day in the marking area, not more than half of them were ever seen on any succeeding day, and most of these were widely dispersed over Cactus Rock and at more distant points.

On the 12 X-marked iguanas, 9 were observed back at Cactus Rock on various succeeding days while the only other one again observed had moved farther away than the release point.

Territory and Aggression

Nonbreeding males approached on other islands and observed at Punta Suarez in 1962 were difficult to get close to and would readily move off when disturbed, showing no strong tendency to return to the area from which they had been driven. The breeding males at Punta Suarez, however, were very reluctant to leave their territories, and when driven from them, would circle about and move back at once to their territories. They appeared quite "uninclined" to leave and could be approached to within two to three feet before retreating, stopping to display at the antagonist as they moved off.

A 200-foot section of the cliff rim at Blow Hole Cliffs had 12 territorial males on February 13. Their sites did not indicate even spacing, but were quite irregular, being as close as 10 feet or with intervals as great as 40 feet between two adjacent territories. No additional territories were observed along this cliff rim over the next six days, though some of these males left the rim (see movement). At least two of these territories included the cliff side below the rim, for active defense was observed in these areas, one centering his activity on a small 1 × 3 foot ledge, 12 feet up from the base of the cliff.

When I arrived at Punta Suarez at the western end of Hood Island on February 12, 1964, the male marine iguanas were very colorful and this, along with their distribution, indicated that it was the breeding season.

There were no aggregations of males, rather, the adult males were somewhat evenly spaced along the rim of the cliff overlooking a large boulder beach along the south side of the point. Below, on the large boulders, and on ledges on the sides of the cliff, males were also on territory.

I had observed the males in this same area in mid-April, 1962, when there was no evidence of breeding territories. I had been impressed at that time by the color of these iguanas in contrast to their congeners on the other islands,

for here they were much more colorful, especially the males, with bodies of red, orange, and black mottling, a turquoise crest from the back of the head to the tail, the front legs also of this color. Then in 1964, these colors were much more intense and contrasting, in effect producing a color pattern which stood out strikingly against the black and dark brown lava. These breeding males could be detected at 200 feet, especially when on the exposed and raised center of their respective territories.

Males encountered on other islands, were much duller in color, frequently showing faint mottling on closer observation, but appearing black at a distance, blending into the background of lava. Inhabitants of the village of Academy Bay on Indefatigable Island have stated that the breeding males become a little more colorful, but do not approach the brilliance of the iguanas on Hood Island.

The territorial male marine iguana passively, by his presence in broad view and vivid color, and actively, by asserting his position through display, declares his presence on his territorial ground. This territory includes a particular area, circumscribed by an imaginary line, which is not only declared but actually defended against the intrusion of other similarly inclined males. It is the territorial male, during the height of the breeding season, that exhibits to the greatest degree the patterns of aggressive behavior characteristic of this species.

Aggression is manifest in a number of ways, singly or in combination; posturing, display movements, head-butting, biting, chasing, tail-slapping, and patrolling of the territory.

The posturing male marine iguana lowers his head, opens his mouth slightly (tongue often showing), and rises up on all four legs (slightly stiff-legged), tail down. The mid-dorsal serrated crest of scales, which is turquoise in color and runs from just back of the head out to the end of the tail, being highest in the neck region and lowest on the tail, is rigidly erect. The height of his crest is enhanced by a mid-dorsal roach of skin raised just beneath the crest on the neck and body regions. The body is inflated and the throat or gular region is bloated and has a small mid-ventral, posteriorly located, wattle or dewlap. In effect, these postural changes increase the size of the lizard when viewed laterally. These changes are the most pronounced when a male is challenging another male at close range (a few inches up to three or four feet). During very intense posturing, when the mouth is one-third to one-half open, a red mark is visible on the tongue.

In general, the territorial males defended areas along the rim of the cliff, on ledges of the cliff, on the large boulders or raised areas of the reef. All of these offered a broad view of the surrounding area, and a male displaying from the highest point of his territory would be seen over a wide area.

On the boulder beach below the cliff, some areas lacked the presence of territorial males, while in a nearby area with larger boulders territories were close together. Three males had territories closely associated with one large boulder about five feet in diameter. One male occupied the top of the boulder, one the ledge just below on the south side, and the other a smaller boulder just below to the west. Two other males were within eight feet; one atop a higher boulder and the other below this boulder to the south. When removed or driven from these sites, they would return directly to them. The close proximity of these territories gave rise to frequent interactions such as displays and short chases.

When challenging another male, the threatening male presented himself laterally to his adversary, thus showing his broadest view and brightest color, and performed display movements.

Such posture was assumed when another male approached close to or entered the territory of the male in question.

During an encounter, each male moved forward a couple of steps, stopped and performed display movements (display-action-pattern or DAP), moved again, stopped, performed, etc., the two males circling about one another one to three feet apart.

Most such encounters did not result in any contact and the male occupying the territory was usually successful in bluffing the intruder, forcing him to retreat from the area.

When contact encounters did occur, the more aggressive male moved quickly from his lateral position head first toward his opponent and attempted to butt him with the top of his head. The top of the head is equipped with enlarged conical scales. The opponent might quickly move a few inches to avoid this charge, but if not quick enough, the aggressor butted the opponent and forced him from the territory by pushing with the top of his head. The opponent might stand his ground, and quickly turn and meet the charging head with his own lowered head. In this position there were two males facing in opposite directions with the top of their heads together, each pushing or butting vigorously. The iguana holding the superior position of height (usually the occupant of the territory) was more often successful in forcing the other back and into retreat. They might reach a stalemate lasting for two or three minutes with their heads together, after which the intruder was forced into retreat. The long claws assisted the opponents in holding firmly to the lava.

Butting contests lasted as long as five minutes, and were often repeated after a few minutes pause. Eibl-Eibesfeldt (1955) reports one head-butting encounter as lasting five hours, interrupted by periods of rest. Schmidt (Shurcliff, 1930) states that butting males may bloody each other's lips, causing a bloody nasal spray. I did not observe any such injury.

When the intruder turned and retreated, the other displayed and sometimes gave a short chase, stopping close to his territorial boundary, from where he again displayed three or four times, then returned to the center of his territory and rested.

A male which was forced to retreat often moved into the territory of another male. He was immediately challenged and continued to flee, entering another territory, was challenged and continued his retreat, etc., in effect running a gantlet of challenging and chasing males until he was outside territorial boundaries. He might then stop and display and continue to move away, or stop and rest. Retreating marine iguanas were also observed running a gantlet of the pecks of adult boobies when their flight took them through the nesting area of these birds along the top of the cliff.

During a chase, if the aggressor caught up to the fleeing lizard, he climbed on his back and rode him, attempting to bite his neck region at the same time.

An aggressive encounter between two males, where both postured and performed display movements, at times set up a "chain reaction" with other territorial males nearby responding to these displays by themselves displaying.

Males were observed apparently patrolling their territories. Such a male moved along the periphery of his territory, moving two steps, stopping, displaying, moving two steps, stopping and displaying, continuing in this manner around its territory. When he came close to a male in an adjacent territory, he intensified his posture. These patrol movements indicated the possibility that territorial males recognize the territorial boundaries of other males, for they confined their movements.

Blue-footed and masked boobies nest along the edge of the cliff and on the flat lava-strewn field above at Punta Suarez. Encounters between boobies and iguanas were inevitable. The bird and lizard, parties to such encounters, usually showed little response to one another, the iguana giving ground to the larger booby, the booby sometimes gesturing towards the iguana as if to peck it. However, when boobies alighted close to a male on territory at the edge of the cliff, they might be challenged, the male iguana holding his ground and displaying at the booby. I did not see a marine iguana cause a booby to leave as the result of such a situation.

The territorial males also responded to my encroachment into or near their territories by posturing and displaying.

When captured and handled, the marine iguana is not readily disposed to bite, but will do so occasionally. Two of our party in 1964 were bitten on the leg, through the pants. These bites were painful and caused a dark bruised area to appear. When a stick or sack is thrust into the mouth of one attempting to bite, the reaction is swift and vicious, giving evidence of powerful jaws.

The territorial male is usually tolerant of females and juveniles within his territory, though juveniles tend to isolate themselves from such areas. On one

occasion a male weakly challenged a female moving into his territory, and this was observed to lead to courtship gestures by this male. At other times, the female moved away as she was approached by the male. Rarely did the male challenge a female or juvenile, but when he did the challenged lizard was moving into his territory, and the resulting pursuits were as long as six to eight feet.

Nonbreeding or bachelor males (less colorful and not defending a territory) formed loose aggregations on the boulder beach and on the cliff side near the feeding reef. Females and juveniles were present in some of these aggregations.

Males established on territories, displayed at one another, but seldom moved into another's territories.

Two breeding males which were killed had an abundance of subcutaneous fat. Such a supply of fat may be an adaptation permitting them to remain on territory for long periods of time without leaving to feed, probably for periods of three or four days or more.

A series of experiments were conducted at Punta Suarez to better observe aggression and territoriality.

Experiment 1. February 13, 1964. When a foreign male was thrown into the territory of another male, the forced intruder immediately fled as the holder of the territory quickly postured. The fleeing male made for his own territorial area, if nearby, and displayed as soon as he was back on his territory.

Experiment 2. A foreign male was held in another male's territory which was up on a large boulder. The holder ran forward and twice butted the intruder (while I held him), then bit the skin of the side of the body of the intruder as he vigorously turned to escape. The defender released his hold when I released the intruder, the latter fleeing.

Another male held and placed into this same territory, first illicited challenge posturing and display by the territory holder and then was rushed and butted, this action shoving the intruder to the edge of the boulder. The aggressor then bit the nearest foot of the intruder. The intruder continually tried to flee, showing no aggressive response.

A third male was introduced in the same manner. The defender moved from eight feet away and vigorously pushed the intruder, then stopped and displayed. This male paid no apparent attention to a nearby female.

The above technique was repeated at a different territory. This time the intruding male was held so that it could be better controlled. The territory holder presented laterally and postured, mouth open and dewlap extended, then performed display movements, quickly moved towards the intruder, and butted him with his head. The intruder was then held rigidly, so that its head met the butting action of this aggressor. The aggressor continued his head butting, but more vigorously, driving the intruder back and he then quickly bit the skin of the intruder's neck and hung on. When I released the intruder,

he fled. The experimenter's head and shoulders were only two feet from this action, yet the aggressor payed little attention to his presence while the other male was present. Once the intruder was gone, the aggressor retreated back into his territory.

The held male was then moved so that he butted the defending male; the defender parried these thrusts by turning his head to meet them head on.

I then swung the held lizard with enough force to knock the defender from his boulder territory. He quickly returned to his territory and resumed his aggressive actions toward the held intruder. When he was knocked from his territory the third time, he appeared exhausted and did not attempt to go back onto his boulder. Later in the day, he was back on his territory.

A small (juvenile—no bright color) male was treated the same as the above breeding males.

This experiment was repeated many times with similar results. The aggressor often tried to bite the neck region after first butting, and would then shake the intruder. The intruder sometimes tried to bite back. One aggressor bit and held onto the foreleg of an intruder; they rolled over and over as I released them. Both could be picked up when biting one another.

A large dull-colored male illicited similar responses when placed in three separate territories.

A female was held in this territory. The male performed head bobs, but did not posture, open its mouth, approach, or attack. The female showed no reaction to the male. The female moved away, crawling over the male, which showed no response.

Experiment 3. February 16. I next tied the legs of a colorful male and placed him in the territory of another male. The latter male responded by posturing, circling, again posturing, and performing head nods; then he quickly charged the intruder head first and butted him from the boulder. The tied male was placed back on the boulder territory and the above actions were repeated, but the aggressor now also bit and shook the intruder, throwing him from the territory.

Experiment 4. February 17. A large male, which was killed for stomach content analysis, was used for the following tests. This iguana was cut up and the head and shoulder region, including the front legs, were kept as a unit. This unit showed male color, but the eyes were closed. It was placed in different male territories. The first male challenged, then butted this unit twice, then showed no more response. The second male butted the unit head on, knocking it off from the boulder. When replaced, he approached the unit, grasped it, and threw it from the territory. The third male attacked the unit immediately with a head-on butt. The fourth male challenged and approached, presenting laterally, then circled the unit with his head down, but then stopped and rested without attacking.

The head was then separated and placed in male territories. Some response was shown, but of much less magnitude than that illicited by the head-shoulders-front legs unit, though it was butted from a boulder a few times.

Many territorial males left their territories during the day to feed on the reef, though there was no consistent pattern, for some made this movement every day, while others were not observed off from their territories over the entire seven days.

When these males were observed out on the reef, they spent much of their time basking. They showed aggression towards one another by asserting with weak displays. When they approached close to one another, they gave little indication of defending a specific territory in this area.

One male which was first observed on territory along the rim of the cliff, also established a territory on an exposure of lava at the edge of the sea near the feeding reef. He moved back and forth between these two territories (100 feet apart) three times in seven days, spending most of his time at the lower territory. However, this lower territory was subject to flooding by the breaking surf at high tide and occupancy by adult sea lions. He was forced to leave during the high tide, but returned when the water receded. He did remain on the territory and defend it with two sea lions present, moving out of their way when they approached. He was forced to leave when the number of sea lions increased, though he moved to the boulder beach nearby and rested there.

When a male moved about his territory, he frequently protruded his tongue onto the lava as if testing. It is suggested that he did this as a means of checking for signs of his own territory or others having been in his territory. The presence of feces on the lava may indicate that the males mark their territories in this manner and that the tongue testing was used as a means of recognition. Similar observations were made by Eibl-Eibesfeldt (1955).

Courtship and Mating

The arrangement of females in the proximity of territorial males at Punta Suarez suggested that many of these males had harems of females. There was no behavior by a territorial male, other than the observation of corralling by one male, that indicated the male took an active part in bringing these females into or keeping them within his territory. It seemed likely that these harems were formed when wandering females moved into the territory of a male. This male did not drive them off as we would another breeding male, and these females thus remained in his territory where the male would frequently court and mate with them. Whether these females returned to the territory of the same male after moving away to feed is not known.

There was no indication of harem groupings of females associated with the males (non-territorial) at Punta Espinosa in 1962 or 1964 (late January), but harems were noted here by Schmidt (Shurcliff, 1930) on January 10, 1929:

"A curious promiscuous polygamy evidently prevails among them, the group of females forming a harem for the old males." Eibl-Eibesfeldt (1955) strongly suggests harems here also.

Courtship behavior was observed every day at Punta Suarez. Most of this behavior was of short duration and did not end in mating.

Courtship gestures by males were observed in territories on flat lava, on large boulders, and on a small ledge fifteen feet up the side of the cliff, as well as off territory.

The courting male approached a stationary female or followed a moving female with his head down. As he moved toward the female from the rear, he nodded his head rapidly (courtship nodding). This nodding is distinct from the movements of the display-action-pattern in that it is more rapid and without definite pattern and with no apparent sequence. Schmidt (Shurcliff, 1930) also noticed this—"The curious nodding of the head which is only slightly modified from the ordinary bobbing of most iguanid lizards, is frequently a part of courtship." As he continued to approach he might circle about the female (as if to corral her) or moved up sideways into contact with her, moving his head along her tail, along the trunk, or both. From this position he then threw his front leg (on the approached side) over the female, moving onto her back. From this position, he attempted to bite the skin of the neck or shoulder region, the necessary hold for continuing with a successful mating.

It was common for the female to move away at any stage of the courtship. The male then might follow and continue to court, or discontinue his efforts.

Males were observed to rapidly approach females and immediately attempt to get a mating hold on the neck. During one observation a male moved up onto a large boulder with two females present. One female fled, but the male quickly grasped a front leg of the other and held onto her, she finally broke loose and fled. One gets the impression that some success in mating depends upon the male's ability to catch the female.

Most courtship observations only went as far as courtship nodding and following.

Copulation was observed on two occasions at Blow Hole Cliffs on Hood Island. The first mating, on February 17, 1964, took place on top of a large boulder. The male had a bite-hold on the skin of the left side of the neck of the female. His right hind leg was thrown over the female, and his body lay mostly over hers, while his tail was twisted under hers. They separated after 15 seconds; the length of time they were *in copulo* previous to this is not known.

The second copulation took place on February 19 in the same vicinity, an area of many territorial males. This mating was more fully observed. The male was within his territory which included the underside, towards the sea,

Figure 2. Marine iguana copulating. Hood Island, Blow Hole Cliffs.

of a large boulder (5 feet high, 8 feet wide) and a flat expanse of lava (15 to 20 feet in diameter) extending seaward from the boulder.

When first seen, the male was holding the female by the skin of her neck and was astraddle her as they walked together across this flat area of lava, circling a couple of times. The male held the female down with his neck-hold and his body positioned over hers. The male twisted his tail, at the same time forcing it under the tail of the female in such a way as to bring the cloacal regions together. His left hind leg was thrown over the female's pelvic region. He continued to hold her down. Intromission could not be seen, but is assumed to have taken place (fig. 2).

They remained in this coupled position for three and one-half minutes, after which period the female made a struggling movement and they quickly separated. The right hemipenis of the male was visible for three seconds, and was then drawn into the tail. The male immediately displayed assertively. The female ran three feet to a raised site on a boulder and rested in an alert posture. The male continued to display a few times for the next minute, then moved to the shade of the boulder within his territory. The whole of these copulatory actions had taken place within his territory and he was not disturbed by males on territory a few feet away.

A copulation was observed in this area on Hood Island on March 3, 1962 by Yale Dawson (personal communication).

Copulation was observed twice by Schmidt (1930) in 1929, on Mangrove Point, south of Punta Espinosa on Narborough Island. These activities took place more than a month earlier than those on Hood Island, between January 7 and 10.

A mating attempt was seen at Punta Espinosa on January 28, 1964, by George Bartholomew.

Display Analysis

The aggressive display of the marine iguana is a species-specific series of movements accompanied by posturing. These displays were recorded both by repeated visual observations with stopwatch recordings and from 16mm. motion pictures taken at normal and slow-motion speeds. The description of the display follows the eight categories of Carpenter (1962); site, position, posture, type of movement, parts moved, units of movement, sequence, and cadence.

The challenge display is the more intense form of the aggressive display and occurs in particular when the iguana is declaring a territory in the presence of an adversary. The female similarly performs on the nesting grounds.

The site of a territory is situated so that a raised station is available giving a broad view of the surrounding area and the male displays from this site. However, when another male encroaches on the boundaries of his territory, the territorial defender will leave this site and move towards the intruder and display in its proximity, this later site being related to the proximity of the intruder.

The position, or orientation, assumed by the displaying male varies with the particular situation. If on his raised territorial site with no intruder apparent, he assumes no particular directional orientation. However, if directing his display towards an intruder at close range (one to three feet), he then orients his broadside (lateral presentation) towards the adversary. The intruder may also orient in this fashion, usually heading in the opposite direction. This configuration of two laterally presented males is termed the face-off position, and is typical of most iguanid challenge displays in close proximity. Such orientation tends to expose the greatest expanse of each lizard and is enhanced by postural changes.

The type of movement consists of a nod or bob, the movement originating at the base of the neck and effecting the head, the tip of the snout describing the greatest distance. Thus, the only parts moved during the display are the head and neck. The amplitude of this movement varies with intensity, but is

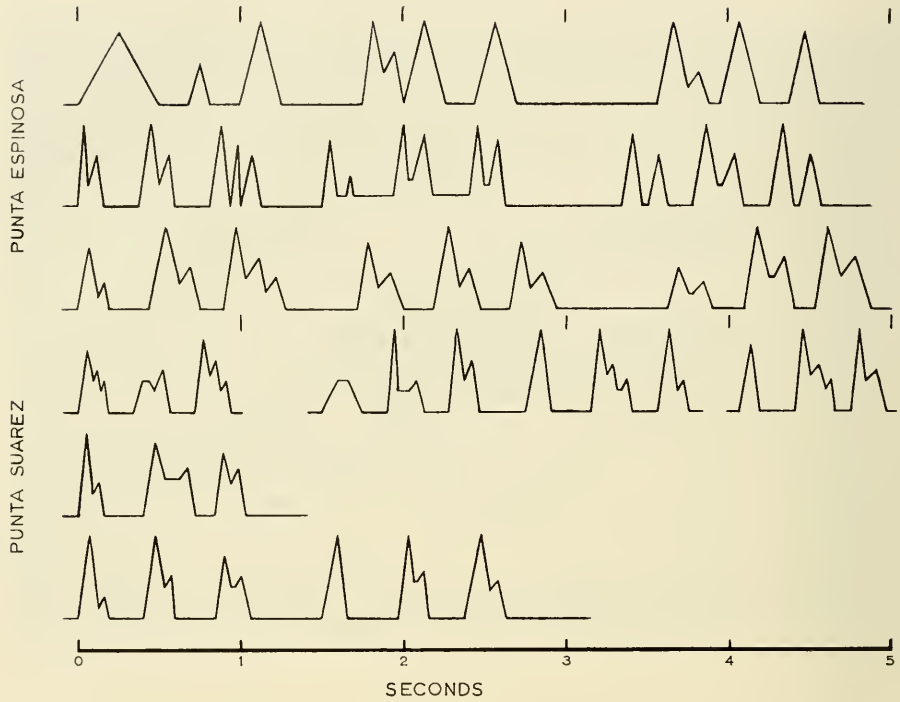

Figure 3. Display-action-pattern graphs of marine iguanas from Punta Espinosa and Punta Suarez. See text for description.

not more than three to four inches from the extremes of the nod. The nod movements are primarily up from the starting position with head lowered.

The units of movement are all similar, though some appear as single nods, some double and some triple. A unit is effected by raising and lowering the head (a single nod), raising the head, lowering and raising again quickly, and then quickly lowering (double nod), or there may be three quick raises and lowerings (triple nod), the later two portions usually of decreasing amplitude.

The sequence of units in the display always occur in a succession of three, but sequences may be repeated in a series up to nine or ten, with very short pauses between.

The speed at which the units are performed during a sequence is the cadence of the display. The cadence of the units varies in the marine iguana from 0.125 to 0.5 seconds, usually falling between 0.2 and 0.25 seconds. The short pauses between units may vary from 0.1 up to 0.3 seconds, most being about 0.25 seconds.

The sequence consists of three repeated nods and these cadence variables produce sequences which range from 0.8 to 1.5 seconds for the performance

of the three units, with an average of 1.1 seconds for over 100 timings, using both stopwatch recordings and slow-motion 16 mm. pictures.

The sequence of movements with its cadence is termed the display-action-pattern and can be graphically represented as a display-action pattern graph (DAP-graph) (fig. 3). Such DAP-graphs are used in comparing the display-action-patterns of the various species of igaunids.

The display may be only one sequence, but three sequences in a series is most usual, with some series running up to nine or ten repeated sequences. Some of the long series may be repeated short series, for the pauses between them are variable.

Though there are no apparent differences in the display movements between the sexes or age groups, the situations for the performance of adult males and females do differ. The challenge displays of the males are associated with declaration of territory and thus are seen less between breeding seasons. The females display primarily during their activity on the nesting grounds. Juvenile displays are infrequent in appearance.

The great majority of displays observed are of less intensity (assertion display) than the challenge display (most intense form). The patterns are the same but the posturing is reduced or absent during assertion displays—little bloating of trunk, mouth closed, body raised on front legs only, dewlap of throat not distended, crest not exaggerated.

A disturbed male moves along the reef for a few feet, stops, performs an assertion display sequence, moves a few feet, stops, repeats one or two display sequences, moves, etc., repeating this until he reaches his destination.

Assertion displays are frequently seen in large non-breeding aggregations. When one male shifts his position within the group, the nearby males may respond by performing assertion displays, but not moving off. Though my data show no significant differences between the displays of the various populations on different islands of the archipelago, and the Narborough Island and Hood Island populations represent the extreme geographical separation of large populations, I believe ("intuitively") that further very critical study will show these two large populations to be developing divergent display patterns. The divergence in these two populations is already very evident in their color patterns.

Communal Nesting Behavior

The nesting activities of the marine iguana at Punta Espinosa were observed from February 26 to March 1, 1962, and from January 26 to February 4, 1964. In 1962, the nesting was in full swing but in 1964 it appeared to be just commencing. Assuming that the nesting periods are similar each year in this equatorial region, the nesting season at Punta Espinosa extends for at least five weeks, and may extend for six or seven weeks. Nesting begins after marked

territorial tendencies have all but disappeared and the males are forming into large aggregations.

The beaches on Punta Espinosa showed no evidence of nesting by marine iguanas on January 25, 1964, nor was any seen during the next day. On the 27th, two shallow burrows were observed which, from previous experience in 1962, were known to be the work of this lizard. On the 28th, two females were observed digging on the beaches in midmorning, one of these being a yellow-spot-marked female from approximately 100 feet away over Cactus Rock. This beach next to Cactus Rock was observed frequently until departure on February 4.

On the 29th, four females were seen digging in late morning and 10 females formed a small aggregation just a few feet up on the lava of Cactus Rock from the beach. Started nest burrows were observed on the beach on the following day also, but no large aggregations of females were evident near by or on the beach. At 8:30 A.M. on January 31, there were no females on this beach. By 9:03 A.M., two females were digging on the beach and more were seen on the nearby lava. At 9:20 A.M., six females were active on the beach, some with well started burrows. In late morning 12 females were on the beach. At 3:15 P.M., no females were active on this beach, while 25 females formed an aggregation on the nearby lava.

Marine iguana females were active on the beach all the following morning, digging burrows, laying eggs, and burying the nests. Some of this activity was still going on at 4:50 P.M. and some nests had been completed. Aggregations of females were very evident on the nearby lava. During the evening, after dark, no females were seen active on the surface, though one female was deep in a nest burrow. She completed laying and burying and had left by 2:30 A.M. the next morning.

No females were on the beach at 6:30 A.M. on February 2. By 8:15 A.M., 10 females were on the beach, one burying a nest while being disturbed by other females. Thirty-five females were on the beach at 8:50 A.M., and many more were at the edge of the lava next to the beach. Thirty-nine were on the beach at 9:10 A.M., and there appeared to be a still larger aggregation at the lava edge, some moving about. A female was seen burying a nest at 1:00 P.M. At 2:00 P.M., almost all females had left the nesting beach, but many burrow starts were evident. At 5:50 P.M. large aggregations were on the lava next to the beach, but no females were on the beach.

The buildup of females on the beach was closely observed on February 3, when it was noted that no females had entered the beach by 7:30 A.M. from the two aggregations on the nearby lava. These lizards moved back and forth between the two aggregations. The first female moved onto the beach, only a few feet away, at 9:03 A.M., three were present at 9:04 A.M., four at 9:05 A.M., six at 9:10 A.M., and nine at 9:17 A.M. The activity in the aggregations on

the lava now was increasing markedly, seemingly stimulated by the presence of the females already on the beach, so that by 9:25 A.M., 80 females were counted over the beach, some entering from another aggregation on another lava exposure 50 feet away. At 10:05 A.M., only 30 females were counted. By 11:45 A.M., nesting activity had decreased further. Some activity continued throughout the day, a few females being present and digging. At 8:30 P.M., 8 females were digging in the dark, while the other females formed large aggregations on the lava.

The last day of observing, February 4, only one of the seven nests started the night before had been completed at 8:00 A.M. Females were seen on the beach. At 12:10 P.M., 50 females were active on the beach, while many more rested on the lava. Fifteen were counted at 3:30 P.M., some remaining on the beach throughout the afternoon, two of these being yellow-marked females from the group previously marked over 100 feet away over the Cactus Rock lava.

The nesting beach at the end of Punta Espinosa showed nesting activity, similar to that seen near Cactus Rock, and this activity was taking place on the same days.

These observations of the buildup of females at the nesting beaches indicated a gradual movement of the females from aggregations on the lava exposures to the area of the beaches over a period of only a few days. Once nesting has started, aggregations of females were continually present on the lava next to the beach from which some moved to the beach and started burrows and then returned to the aggregation. I think that these females remained in these aggregations for at least three or four days or longer before successfully digging a complete burrow and laying their eggs.

A female usually moved out onto the beach and wandered about, stopping and watching from an alert posture, then wandering again. She might continue this pattern for 15 to 20 minutes and then move back to the lava. When a number of females were on the beach at one time, they were apparently very aware of one another's presence, often approaching one another and displaying aggressively by performing head nods. The number of females on the beach at any one time varied, as they came down from and returned to the nearby lava. Less than twenty-five percent of the females on a beach at any one time were digging a burrow, though one might dig awhile, get in a squabble with another, and be driven off.

The presence of a number of females active on or moving over the nesting beach at the same time, especially digging nest burrows in close proximity to one another, initiated aggressive actions. When two females attempted to dig at the same burrow simultaneously, a squabble invariably resulted.

These aggressive actions involved one or all of the following: threat, posturing, chasing, display of head nods, biting, and head butting. When two females approached one another within one or two feet, one or both assumed a

threat posture by rising stiffly on all four legs and opening the mouth slightly. One or both then might perform head nods. Both usually moved off from this type of encounter without any further action. The partially opened mouth was the most common type of aggressive indication.

When a wandering female approached a female digging a burrow, the resident showed a threat posture first and might follow this up by attacking the intruder, the latter then fleeing. Often the approaching female would move in and try to dig in this burrow and this incited the resident female to try and bite the intruder or to lower her head and lunge at the intruder with a butting motion. If this did not drive the intruder away, the butting motion was carried forward to contact with the aggressor pushing the intruder with the top of her head. This might have the effect of turning the intruder on her side or back. The resident female had the psychological advantage and usually won the encounter, the intruding female retreating. Infrequently the intruder might meet the challenge by also lowering the head and lunging head first at the resident female. Where they then met head on they attempted to push one another backwards, or one gained an advantage by getting her head against the body of the other and forcing the latter to roll over. During such a melee, which moved back and forth over a couple of square feet around the burrow, attempts to bite were made by both parties. When both moved back to the burrow and tried to dig, the squabble would commence again.

As many as three (and probably more) females in succession may try to dig at the same burrow, one being driven away by another. This implies that a wandering female coming upon an already started burrow might start to dig, although she had not previously been to this burrow. It is probable that many females did not lay their eggs in the burrow they originated. Also, many more burrows were started than were ever completed. Many burrows were caved in by squabbling females, for unless a burrow was started away from the group, the digging female was continually disturbed. Some females, when disturbed by me, retreated to the sea, while others moved away over the sand, stopping frequently to nod aggressively.

Once the burrow was well started, about one foot in length, or was completed or near completion, the female was less easily disturbed. The laying female was reluctant to leave her burrow.

Nest Sites, Nest Construction, and Egg Laying

There appeared to be no special set of conditions on the beach on which these lizards chose to dig a burrow except that it be above the high-tide line. All burrows observed were above the drift line formed by the high tide. Breakers from a heavy sea would, however, bathe the sand above many nests. The distribution of over one hundred points where females had dug (not necessarily completed) were scattered all over the beach. Many burrows were

started on a slight incline, but so much of the beach inclined one way or another, that this appeared unimportant. Others were dug where the sand was flat. The direction taken by the burrow and its opening showed no consistency and it often appeared to be related to the direction from which the female moved onto the beach.

In beginning a nest, the female began to scratch alternately at the surface of the sand with her front feet, throwing sand back, with some going laterally. Soon a small concavity appeared and the digging effort was concentrated towards the center of this, still using the front feet. If an obstacle was encountered, such as underlying lava, digging attempts might continue for a few tries, but then this start was abandoned. If the female was disturbed when the concavity was only a few inches deep, she might also abandon it. As the burrow became deeper, she was more reluctant to leave and abandon. I purposely disturbed females which had well started burrows and drove them away for 10 to 15 feet. Most of these females returned to the same burrow.

As the nest burrow became deeper, the hind feet were also employed. The sand was thrown back by the front feet and then pushed farther back with the hind feet. As the sand accumulated near the entrance of the deepening burrow, the female turned around, facing away from the burrow, and used the front legs and pectoral region to push the sand away from the entrance for a few inches. Periods of digging were interspersed with short periods of rest, either down in the burrow or at the entrance.

The top of the burrow frequently caved in as the female dug, which necessitated further effort or a new start. Sometimes the cavein was such that the lizard was trapped and held by the sand and she had to struggle to back out of the burrow, sometimes not succeeding (see mortality).

When there were a number of females on the nesting ground at the same time, the nest burrows might be in various stages of construction; some females were starting nests while others were covering nests. It took a female at least three to four hours to dig a nest hole and lay her eggs. During this time, however, she might leave and return.

When the female had completed the digging of the nest burrow, she then assumed the laying position by heading out of the burrow, her pelvic region near the inner end of the burrow and her tail curled back out towards the entrance. Usually the head of the laying female was visible at the base of the burrow, though some were not visible, the latter being determined by reaching into burrows and feeling laying females present. Laying females were not easily disturbed. As one watches these females they move now and then as if in labor.

The following is an account of observed egg laying at Punta Espinosa: in the late afternoon of February 27, 1962, we were able to dig a side tunnel into a nest burrow which was occupied by a female (undisturbed) about to start laying. The posterior of the female was visible through this opening. Her

tail curled back towards the entrance so that her hind legs and pelvic region rested about four to six inches from the inner end of her burrow. This was at 5:10 P.M. No activity was noticed until 5:25 P.M., at which time she intermittently wiggled and contracted the abdominal region, slightly shifting her hind legs. At 5:26 P.M., the pelvis was slightly raised and arched by the hind legs. The cloacal opening began to expand. Then over a period of about 30 seconds, and with a series of more vigorous abdominal contractions (my field notes say "grunts"), an egg emerged little by little with each contraction, moving completely out with the fifth. She then wiggled her pelvis from side to side, which loosened the egg from the cloacal lips. The egg appeared to be very soft. The female's actions caused some dirt to cave into the nest. The female appeared to be resting for a few seconds. Then, again, the intermittent abdominal contractions and shifting were repeated. At 5:37 P.M., the second egg emerged, but faster than the first egg, "popping" out in a couple of seconds. The female pushed these eggs posteriorly with her hind feet, and then rested. Soon more contractions and shifting. The third egg emerged fast and "easily" at 5:43 P.M. The female again wiggled her pelvis from side to side. Her abdomen appeared to be very sunken. At 5:50 P.M., the female began pushing sand back with her front feet, which caused sand to cave in on her. She was filling sand into the inner part of the nest when I disturbed her and she ran "reluctantly" from the burrow.

Filling and covering of the nest burrow begins soon after the last egg is laid. The female starts by scratching backwards with her hind legs. She begins to move out of the burrow as she does this. This movement out is indicated by the state of the deep end of the burrow when the nest is dug up. In no instance did I encounter eggs which were packed in sand, rather they all were partially exposed in an open chamber at the inner end of the burrow, or loosely covered with sand. The eggs are usually one to two inches from the inner end of the burrow. The adaptive significance of this is apparent, for the hatching lizard must have a little freedom of movement to emerge from the egg and start its digging ascent to the surface. However, the tunnel leading out from this chamber is tightly packed.

As the female continues to scratch sand into the burrow, now with the hind feet, then with the front feet, she moves part way out of the burrow in doing this. This scratching caves in some sand from the sides of the burrow. Soon she comes all of the way out of the burrow and turns around and pushes sand into the burrow using both the head and the front feet. She then moves forward into the burrow and rams the sand with the top of her head; the effect of this butting action packs the sand solidly into the now filling tunnel. In this manner, she slowly works her way out of the disappearing burrow. She moves to the side of the burrow entrance, scratches sand back with the front feet, then turns and pushes it farther with the head, front feet and legs,

propelling with the hind legs, then rams the sand with the top of the head. As the burrow fills more and more, she moves farther from the entrance to move sand back for fill.

When the burrow is filled so that only a slight concavity is apparent on the beach, she continues her efforts by crawling back and forth over this area, sometimes pushing sand. Once the burrow filling is completed (even with the surrounding area) she still continues to move back and forth over the spot in an ever widening circle, scratching sand, usually with the front feet, to be followed by the hind feet, moving sand in many directions.

She continues to scratch randomly over and around the nest area for five to ten minutes. When I disturbed one female in this stage of burying, she moved off about thirty feet, bobbing aggressively, and circled about me, stopping to scratch. When I moved off, she returned to the area and continued scratching, even though it was almost impossible for me to discern where the entrance had been. When she was circling out from me, away from the nest area, she continued to scratch.

During the burying process, a female, when at the surface, reacts very aggressively towards other females which approach her, by opening her mouth, displaying head bobs, and sometimes charging at the approacher and driving her away, trying to bite the retreating lizard.

Nest entrances that I had marked were indistinguishable once the female had left the area, amazingly camouflaged, the sand packed solidly.

The urge to cover the nest was intense, for females moving at random over the beach, were observed stopping here and there to go through scratching movements. Such actions were also observed in females which had just had an aggressive encounter with another female (possible displacement behavior).

Once the nest is buried, the eggs are well protected. We attempted to stamp heavily on the sand above a known nest chamber, but could not cave the sand in. Sea lions, weighing many hundreds of pounds, frequent this beach throughout the year and are active both day and night during the nesting season, the nest burrows are well adapted to protect the eggs from this hazard.

Once nesting activity had built up, it continued off and on both day and night. On the night of February 28–29, 1962, many females were moving about the beach, some digging. On the nights of February 1 and 3, 1964, females were active on the beach in the dark, some digging. One of these burrows was marked at 10:00 P.M. when the female was in the burrow laying. When checked again at 2:30 A.M., the nest was completed and the female gone. Most of the nest had been dug and completed in the darkness.

Evidence of marine iguana nesting was observed at seven localities on five islands and each area provided a varying set of conditions.

The first indication of nesting occurred near the Charles Darwin Research Station on February 14, 1962. A female had moved back away from the reef

to the edge of the clearing where I had placed my lizard enclosures. She was first seen digging at 9:00 A.M., and had started three different holes. When approached, she quickly retreated into a small cave in the lava near by. On the following day (15th), I noticed her come from the brush into the clearing shortly after 10:00 A.M. She moved very cautiously, then began scratching as if searching for a place to dig, then stopped, displayed, looked about, and then dug some more. Following this pattern, she moved about the edge of the clearing over an area of about 300 square feet. She moved to the shallow holes she had dug the previous day. When again disturbed, she retreated to the same small lava cave. On the 16th she was again observed active in this area at 9:15 A.M. On the 17th I did not see her, so at 10:00 A.M., I examined the lava cave and she was resting at the entrance. On the 18th she was seen as she retreated to this cave. When observed in this area on the 19th it appeared she was becoming emaciated. No good burrows had been dug at this time in this area and when I returned 12 days later, there was no evidence of her presence, though she may have nested and left.

Nesting activity was observed on the beaches east of the Charles Darwin Research Station on February 22 and 23, 1964. Many nest burrow starts were noted in the sand just inland from the boulder beaches in this region. Many burrows appeared abandoned after encountering lava boulders or mangrove roots. Two burrows were observed which were nearly completed. The females in this region probably make a number of attempts before successfully digging a burrow.

While visiting a small reef island (Devine's Island) in Academy Bay on February 12, 1962, numerous diggings were noted. This small islet (450 × 200 feet) is a bar of coral sand that has been piled up on a lava reef lying only about 50 feet from the shore of Santa Cruz Island. It is now rimmed by mangroves, with patches of low succulent vegetation scattered over the sandy interior of the islet. Later observations on other islands confirmed that these diggings were those of the marine iguana. I counted 40 diggings varying in degree from hollows scratched in the sand to well dug oblique burrows a foot or more deep. The openings were 8 to 12 inches wide and 4 to 6 inches high. The tail tracks of iguanas were evident at many diggings.

Jensen Island lies about one mile off shore at the entrance to Academy Bay. This island, formed from a large lava reef, covers approximately 15 acres. The margins of the island are higher and vegetated by low succulent vegetation, while the interior forms a basin and is only sparsely vegetated. When first visited on February 24, female marine iguanas were seen, and freshly dug holes were numerous over the open sandy interior of the island. Fifteen of these burrows were examined, but no eggs were found. On March 13, no females were observed in the interior of the island, but many open burrows were present. It appeared that the marine iguanas had completed their nesting

on this island. No nesting activity of any type was observed on April 6.

Burrows in various stages of construction were also observed on Jensen Island on February 24, 1964, in the same area noted in 1962. Aggregations of iguanas were within 20 to 30 feet in the vegetation.

On the morning of February 25, while anchored in a small cove at Point Vincente, on the northwest coast of Albemarle Island, I noticed a marine iguana on the top edge of a 50- to 60-foot cliff on the north side of the cove. Curiosity as to why this lizard had sought such a position led me, by a circuitous route, to the top of this cliff. Here, the area was a gradually sloping incline which ascended for about 1,000 feet to sheer cliff. Much of this high sloping plateau was covered with a black lava sand or dirt which was very dry and dusty. The scattered shrubby vegetation appeared wilted owing to the extreme dryness. Blue-footed boobies were nesting along the cliff edge.

One nest burrow was being excavated by a female, while 50 to 60 open or partly open burrows were scattered over the slope, some in the open, some beneath lava boulders and some beneath shrubs. Probably there were many nests which had been completed. The sand, a few inches deep, had some moisture content. There were 20 to 30 females present on the slope, resting in the shade of the vegetation.

One-quarter of a mile along the edge of this cliff, in a thicket of *Opuntia* cactus and scrub were signs of marine iguana nesting activity. It appears that these lizards use any available site which provides enough soil in which to dig a burrow and will migrate one-half mile or more inland and up steep cliffs to do so.

When at Punta Suarez on Hood Island, April 17, 1962, nesting activity was observed, but not as intensive as that observed at Punta Espinosa on Narborough Island. In this area of this island, there is very little open sandy area that is above the high-tide line. All nesting signs were on the plateau area above the cliffs to the south side of the point. This plateau is strewn with lava boulders with small patches of hard gravelly soil present here and there. The vegetation is scant and short except for patches of shrubs. It is in this area, at this time, that there were numerous nests of the blue-footed and gray-footed boobies, and also the beginning of the buildup of the nesting colony of the waved albatross. Iguana nesting signs were interspersed at random between these birds' nests. Any iguanas moving over this area would certainly encounter birds on their nests. Yet, numerous diggings, similar in size and shape to those observed at Punta Espinosa, were scattered over the area. Most of these excavations appeared to be unsuccessful attempts, many burrows being shallow with lava blocking the way to further digging. A female was observed in one of the deeper burrows on this date (fig. 4). (At first I thought that these might be retreat burrows, but later experience in the same area in 1964

Figure 4. Female marine iguana (containing large eggs) digging nest burrow on gravel-strewn plateau above Blow Hole Cliffs. April 17, 1962.

made me feel certain these were nest burrows.) Females were observed in the process of digging, much effort being needed in this hard and scant soil. Many burrows went under large lava boulders where it was possible some success could be achieved. No eggs were found in the burrows examined (open burrows) and no completed burrows were located. Captured females in this area contained large eggs.

To get to this area from the seashore to the south involved climbing up the cliff and inland movements of 10 to 200 feet. However, the iguanas in this area in 1962, customarily formed aggregations along the upper edge of the cliff.

The presence of numerous juveniles at Punta Suarez, is evidence that nesting is successful in this area.

At this same area on Hood Island from February 12 to 19, 1964, no signs of nesting activity of the marine iguana were observed. Neither were any observed on the east end of this same island, nor on Gardner Island, just off the north coast of Hood Island, although both the latter areas had aggregations of marine iguanas. However, wherever marine iguanas were observed on this island at this time, males were very actively defending territories.

When the nesting periods of Punta Espinosa on Narborough Island and Punta Suarez on Hood Island are compared, these observations indicate at least a month's difference in the breeding season, that on Hood Island, the southeastern most island of the archipelago, lagging behind the populations found on the western islands: Narborough, Indefatigable, Abingdon, and Albemarle. Karl P. Schmidt (Shurcliff, 1930) records the breeding season as being in full swing on Narborough Island on Jaunary 10, 1929, the males spread out on territories and actively courting females. Very little evidence of territoriality was observed on this same island in late January, 1964, and late February, 1962.

The 12 nest burrows measured at Punta Espinosa ranged from 22 to 24 inches in length (mean of 23.6 inches) and the chambers at the inner end of the burrows varied from 10 to 16 inches below the surface (mean of 13.4 inches).

A total of 16 nests were excavated (10 in 1962 and 6 in 1964) at Punta Espinosa from which 29 eggs were removed. One nest contained six eggs, three had three eggs each and the remaining 12 each had two eggs. It is my belief that the nest with six eggs represented probable clutches of three from two different females. Three additional eggs were laid by females held in captivity.

The 38 eggs measured ranged from 7.8 cm. to 10.00 cm. in length (mean of 9.3 cm.) and from 4.02 to 5.15 cm. in width (mean of 4.2 cm.). They ranged in weight from 79 grams to 121 grams with a mean weight of 96.28 grams. Some of the variation was without question due to absorption of water, causing increases in all measurements, though the figures for most eggs were recorded less than four hours after nest completion.

The eggs are white and the shell is leathery in texture. They have the shape of a blunt oval, both ends being equal.

The aggressive actions of the females on the nesting beach are similar to those of aggressive males declaring and defending their territories. The female does not show the elaborate posture of the male, but her performance of the display-action-pattern, threatening with open mouth, biting, riding, and head-butting encounters are essentially the same as those of the male.

Since a female is often disturbed while digging and may dig in a number of places, including excavations started by other females, the territory is not a stationary point or area, but a transitory area about the female that moves with her wherever she may be on the beach.

So far as I have been able to determine, the marine iguana is the only communal nesting iguanid, and perhaps lizard. This may be partly because of their gregarious tendencies in the non-breeding season. A. L. Rand (personal communication) has data which suggest communal nesting for *Iguana iguana* in Panama.

There appear to be optimum areas for the survival of this species, in particular protected lava reef areas with associated beaches or areas of soil near the sea. The beaches and areas of soil are limited on most islands of

the archipelago and thus must be fully utilized. The scarcity of good nesting sites would tend to bring the females together in these areas when they are ready to dig burrows. The female territorial activities may have evolved in association with these nesting aggregations on communal nesting areas.

The spread of nest burrows and burrow attempts over all of the available area offers adaptive advantages. If females dug burrows in close proximity, there would probably be many nests destroyed as other females dug into them. Their separation would also lessen their chance of being destroyed by sea lions. On the emergence of the young later in the season, these hatchlings would already be scattered and less available to predation than if they emerged and formed aggregations. The aggressive actions of the nesting females would contribute directly to spreading out of the nest burrows.

On two occasions, when digging up nests, egg shells from previous years were encountered at nest chamber depth, indicating successful hatchings from previous years. Old egg shells were also seen on the beach surface, probably dug up by nesting females.

The nesting females had to contend with the ponderous sea lions which used the same beaches for basking in the day time and for resting at night. Sea lions moved all across these beaches and were observed to cave in partially dug burrows and at times rest immediately over them. The females moved away from the sea lions and could not possibly challenge their movements. Once the nest was completed, however, they were safe from disturbance by the sea lions.

In one nest, the two eggs present were stuck together. Small maggots were seen between the eggs, indicating that parasitism may destroy some eggs.

Though most nests were constructed above high-tide line, a high surf did send waves crashing over areas of known nests. Undoubtedly these eggs are adapted to frequent bathing by salt water. Such bathing by salt water would also take place at nesting areas on Jensen Island, Indefatigable Island, Devine's Island, Bindloe Island, and probably many other localities. Such relationships of the egg to salt-water bathing need further study.

The digging of a nest burrow could be a hazard for the female. In 1962 at Punta Espinosa while observing the female activities on the nesting beach, I noticed the tail of a marine iguana protruding from the sand, no other part of the lizard visible. I pulled on this tail which showed no response, and I assumed the lizard was dead. It appeared to be a female which had been digging a burrow and the sand had caved in and pinned her so that she could not escape. I returned one hour later and pulled this female out of the sand and found her to be alive. I later noticed a similar situation, a protruding tail, and when this female was pulled from the sand she was dead. Another which was observed had a tail only visible in an obviously caved-in burrow. She was alive and when I returned later, she had escaped from her predicament. On

the beach at the end of the point, I dug up a caved-in burrow with a protruding tail, intending to photograph this, and found the female to be long dead, all but the protruding tail in an advanced stage of decay (bone with some dried flesh). It is very probable that many females die as a result of caved-in burrows, especially in nesting areas of coarse and loose sand. It is possible that dead females that I observed washed up on the beach here had met such a demise.

A female, observed on February 2, 1964, had her burrow cave in on her while she was laying eggs. When later checked and dug up, she had finished laying and escaped, probably because she was headed out, rather than in.

There is no evidence as to exactly how long the marine iguana eggs must incubate before hatching. However, from bits of evidence from various sources, I believe it to be a minimum of two months and possibly three months or longer.

Since it seemed that I was present at the beginning of the nesting season in 1962 (late January), the appearance of the first hatchlings would be evidence of the approximate period for incubation. Miguel Castro has been at Punta Espinosa in April and has seen the hatchlings emerging from the sand. He thought these were some of the first to hatch.

A hatchling, with prominent umbilical scar and evidence of abdominal yolk, was seen emerging from beneath the large coral sand beach at Tortuga Bay on Indefatigable Island on May 17, 1962, by Sigvart Hornemann. Since female iguanas were digging nest burrows in February on this island, this would indicate more than two months for incubation.

Eggs collected at Punta Espinosa in late February, 1962, were kept in damp sand from this area and taken to the Darwin Research Station, and later, those that remained, to the United States. Eggs cut open on May 27, had living embryos only about two-thirds developed (after three months of incubation). Though the remaining eggs spoiled in my laboratory in Oklahoma, some were still alive, but not fully developed in early July. No doubt the conditions which I provided for incubation extended the period, but still these gave evidence of a prolonged incubation of over three months.

Eggs of the Galápagos lava lizard (*Tropidurus pacificus*) laid and incubated under simulated natural condition in Oklahoma, took 123 days to hatch, much longer than the eggs of other species incubated under the same conditions at the same time (62 to 75 days). If this much smaller lizard requires a long incubation period, this may indicate the marine iguana of the same area has a longer period.

Eggs of marine iguanas collected from February 2 to 4, 1964, at Punta Espinosa, were again kept in their natural sand and taken to the United States, by sea and air, to my laboratory in Oklahoma. None hatched successfully,

but some appeared to be still alive in early July. When opened, they were not fully developed (over four months incubation).

Miguel Castro, in describing the emergence of the hatchling marine iguanas at Punta Espinosa, states that they apparently burrow straight up from the egg chamber. On one occasion, one emerged beneath his sleeping bag during the night. He states that others he has seen during the day, on reaching the surface, look about, then quickly head for the mangroves or other types of cover. He wondered why they moved off so quickly until he saw gulls and herons fly in and feed on them.

Hatchlings and small juveniles observed at other places by me in May were always near vegetation, such as mangroves, and near the edge of the water.

Associations, Predation, and Other Observations

Darwin thought it anomalous that these aquatic lizards could be driven into the sea only with difficulty, permitting themselves to be captured before entering the water. I found them to be somewhat reluctant to enter the water, but once cornered near the water's edge, they did not hesitate to take to the sea and swim out to deeper water. They sometimes swam along on the surface parallel to the shore and at other times swam up to 50 feet under water, moving along the bottom in shallow water. They did not hesitate to swim across lagoons to reefs on the other side.

When startled or pursued in areas where deep crevices were present, they readily retreated into these, moving down the steep sides. If I attempted to reach them, they then moved along the crevice wall at the lower levels. At Punta Suarez, they would quickly scamper over and down the side of the cliff.

Those marine iguanas on Indefatigable Island and small Jensen Island, that dwelled on flat reefs continued shoreward by thick shrubby vegetation, retreated to these thick clumps when pursued.

In areas where the reefs were fringed by mangroves, many iguanas, especially at high tide, climbed into these trees and rested. Others retreated up into the mangroves at night.

As many as 70 juvenile and adult iguanas basked daily on the near-perpendicular sides of a 30-foot cliff at Punta Suarez. To maintain their basking positions, they had to hang on with their claws. Some would remain here for an hour or more.

When approached singly or in groups, the adult marine iguanas commonly snort or spray a fluid from their nostrils. This fluid is ejected with force and may shoot for a distance of more than a foot. When a group is startled and a number of lizards eject at the same time, it is a weird sight and startling in itself. Because it comes as an element of surprise it may act as a type of threat or distraction behavior. Iguanas will eject this fluid when not disturbed,

but in this situation, usually do so as they rouse from basking or change basking positions.

However, such behavior probably is primarily a function for the lizard to get rid of salt. The marine iguana is provided with a pair of glands lying subcutaneously between the nostril and the eye (Schmidt-Nielsen, 1958). While feeding on the salty aquatic vegetation, either above or below water, the iguana takes in vast quantities of salt water, which would tend to greatly increase the salinity of the tissues of the lizard. The salt gland extracts the excess salt and the iguana ejects it from its nostrils, into which the salt glands open.

There are a number of animals that live in close association with the marine iguanas. At Punta Espinosa on Narborough Island, these included the sea lion (*Zalophus wollebacki*), the Galápagos fur seal (*Arctocephalus galapagoensis*), the flightless cormorant (*Nannopterum harrisi*), the Galápagos penguin (*Spheniscus mendiculus*), the pelican (*Pelecanus occidentalis*), one of Darwin's finches (*Geospiza difficilis*), the lava lizard (*Tropidurus albemarlensis*), the green heron (*Butorides sundevalli*) a Galápagos snake (*Dromicus sleveni*), and the very abundant red crab or sally-lightfoot (*Grapsus grapsus*). These frequent the same reefs as the iguanas. The Galápagos hawk (*Buteo galapagoensis*) visits these areas.

At Punta Suarez on Hood Island, in addition to many of the above, the iguanas I observed live in close proximity to nesting blue-footed boobies (*Sula nebouxi*) and masked boobies (*Sula dactylactra*), and mocking birds (*Nesomimus macdonaldi*), and the two finches, *Geospiza fuliginosa* and *G. conirostris* move among the iguanas. Here, swallow-tailed gulls (*Creagrus furcatus*) nest on the side of the cliff frequented by iguanas. The plateau (and other areas of this island) just above Blow Hole Cliffs is the only known nesting area for the waved albatross (*Diomedea irroratea*). Short-eared owls (*Asio galapagoensis*) forage in areas where the iguanas are present.

All of these animals are generally tolerant of one another and the interactions between the iguana and most of these associates were few. They basked and rested within inches of one another.

I have seen lava lizards running over iguanas, even resting on their heads, the iguanas showing no response. Perhaps the lava lizards were attracted to the flies which are sometimes present around aggregations of iguanas.

Red crabs are abundant on all reefs of the Galápagos Islands and intermingle with iguana aggregations, crawling between and over them, feeding near to them, and retreating into the same crevices. I did not see an iguana respond to the presence of a red crab, though a lava lizard was observed eating a small individual of this species.

Iguanas which were basking close to sea lions frequently had to move quickly as a sea lion changed its position. I did see a sea lion roll over an

iguana, the latter appearing quite "ruffled" but able to run away. This was on a sand beach. If such had happened on lava, the iguana probably would have been crushed. Usually the iguanas lying near sea lions move just enough to stay out of the way.

Boobies may peck at iguanas moving near their nests and as mentioned previously, a male was observed apparently displaying at a pair of boobies resting on a boulder in his territory.

Very few observed predations on marine iguanas have been recorded, and the large numbers and success of this species have been stated to be partly due to the lack of predation. There are, however, a number of species quite capable of preying on the marine iguana at some stage of its life.

Raymond Levegue (personal communication) reports that mocking birds were observed pecking into the eggs of marine iguanas on Hood Island, immediately after laying.

Miguel Castro, a long-time resident of Indefatigable Island and a keen observer of animal behavior, has seen newly emerged hatchling marine iguanas being attacked and devoured by gulls and herons.

I have observed six-foot sharks swimming in water where marine iguanas feed, and have seen large iguanas with as much as two-thirds of their tails missing, perhaps lost in an encounter with a shark.

The Galápagos hawk (three individuals) was seen foraging at Punta Espinosa during each day of our stay in 1964. A nest of this hawk, located in 1962, was within one-half mile of the point and was still active in 1964. In 1962, a near fledgling young bird was on the nest.

Seven incidents observed at Punta Espinosa in 1964 indicated predation by the Galápagos hawk. On January 27, I noticed a hawk on Cactus Rock feeding on something, which on closer approach and with the aid of field glasses, proved to be a juvenile iguana. It was seen to move, as if still struggling. The hawk flew from my closer approach, but alighted about 100 yards away and continued to feed.

Another hawk flew over the point on January 29 carrying a small iguana in its talons; it appeared limp but fresh. On January 31 a hawk was seen rising from the edge of a large crevice with an iguana. It flew to a dead mangrove, alighted, then bit the neck area of the lizard and proceeded to tear apart its prey and devour it.

A hawk was feeding on a dead iguana next to our camp on February 3. Just before noon on this same day, a hawk swooped in on the beach near camp, landed, ran five to six feet and grasped an adult female marine iguana which was performing nesting activities. The hawk hung on near the neck and shoulders with its talons and rode the now rapidly crawling lizard, for about five feet, then let go and stood on the beach for a few moments before flying off. As this hawk flew in on the beach, the iguanas on the beach scattered,

most of them running to the lava close by. In the early afternoon and again in mid-afternoon, a hawk again swooped over the beach, and the female iguanas quickly retreated, one female 150 feet away running quickly the 30 feet to a reef. I also saw this hawk carrying and eating a snake found on the point.

Of the domestic animals introduced by man and reverted to a feral existence on the Galápagos Islands, the house cat and the pig probably prey to some extent upon at least small iguanas, and in the case of the pig, upon the nests.

Though man does not find the marine iguana good eating, this is probably the fate of some, and Slevin (1935) records that sailors were known to eat them.

The carcasses of iguanas provide carrion for both red crabs and the Galápagos hawk (*Buteo galapagoensis*). The red crabs, usually large individuals, are always present on those carcasses seen near the water.

Carcasses at a distance from the water were seen to be visited by the hawk, which stood beside the lizard remains and proceeded to tear away pieces as it held it down with a foot. It swallowed these pieces immediately. After feeding, the hawk flew away, but returned to feed again.

There were always some iguanas that appeared to be shedding, for many showed blotches of light-colored loose skin. I observed one scraping its head on the lava, apparently trying to rid itself of loose skin.

On two occasions, when a helicopter brought visitors to our 1964 camp on Punta Espinosa, the marine iguana responded by scattering in apparent confusion. Whether this response was due to the soaring presence of the vehicle or to the loud noise of its engine, was not certain.

Of the many hundreds of marine iguanas observed on the Galápagos, I only saw one which appeared decrepit. It was very emaciated and moved very feebly, and was perhaps a very old individual. Externally at least, these animals appear to be quite free of disease.

A frequent observation at Punta Espinosa in 1964, was an adult iguana coughing violently and shaking its head, as if trying to regurgitate. I never saw anything regurgitated. After a coughing spell, sometimes as many as 20 attempts, they may swallow a few times. It is possible that this coughing may be due to intestinal or respiratory parasites, or perhaps a gastric disturbance.

The common occurrence of ticks of the genus *Amblyomma* (identified by Hoogstraal, 1964) on the marine iguanas has given rise to a unique relationship between these lizards and certain small birds.

Deticking behavior was seen to be done much more frequently by finches in 1964, both at Punta Espinosa and at Punta Suarez. At the former, the finch was identified as *Geospiza difficilis,* one of the smaller Galápagos finches. On Punta Suarez, two finches were present, most of this activity being performed by the smaller form, *Geospiza fuliginosa,* less frequently by *G. conirostris.*

These small birds moved freely among aggregations of iguanas, hopping alongside, on top, and along the backs of the lizards. The sites at which they

showed most interest and pecked were those areas most frequented by ticks; the neck, axilla, groin, and cloaca. After moving through one group, a finch sometimes flew 10 to 20 feet to another group and continued its searching behavior. On one occasion, a small finch pushed the tail of an iguana aside. One finch examined 10 different iguanas during one minute. The iguanas showed no response to the activities of these finches.

A tick was found in the throat of a finch (*G. difficilis*) collected while hopping among a group of iguanas.

During the early morning of February 21, 1962, on the southern coast of Bindloe Island, as I was observing a group of marine iguanas, a bird flew up and lit near an adult iguana. This mocking bird then hopped up next to the iguana and pecked at the shoulder region and then in its axillary region. I assumed at this time, and I believe correctly, that this bird was searching for and removing ticks from the iguana. The bird put its head into the iguana's axillary region and appeared to twist its head, as if to tear a tick loose from its solid hold on the hide of the iguana. The iguana appeared to be completely indifferent to this activity of the mocking bird, completely tolerant. This bird then flew a few feet to another iguana and repeated the searching and removing motions. While I watched, the bird continued to move among the group of iguanas over a space of 20 to 30 feet, examining closely at least three of the lizards. Mocking birds were observed performing similar actions at Punta Suarez in 1964.

Beebe (1924) refers to land iguanas (tussled) being deticked by mocking birds. Beebe also records a red crab removing ticks from a marine iguana.

In areas on lava exposures frequented by the marine iguanas, the lava was stained by their excrement, a mixture of white (uric acid) and greenish-browns (from the alimentary tract). The feces pass as a semi-fluid or watery material, sometimes ejected with an audible squirt. Many iguanas in large aggregrations are themselves soiled with blotches of excrement. There appears to be no special location for elimination, except for the possibility of sign posting in territorial males.

When defecating, the pelvic region is raised by extended and outwardly presented hind legs. This raises the base of the tail as the feces pass out. These iguanas made no investigation of their own feces, at least just after passing such.

The walking gait of the iguana is an alternate forward movement of one front leg, followed by the hind leg of the opposite side, then the other front leg followed by the other hind leg; typical quadruped walking. It uses the same gait when running and one can move over rough lava about as fast as a man can safely run.

When walking over a reef, an iguana sometimes gets a claw temporarily stuck in the porous lava, and must jerk to release it.

The quiet lagoons and sheltered areas of exposed reefs did not have large aggregations of iguanas, but rather, the largest aggregations occupied areas just beyond the reach of heavy surf. Though not as adapted as the sea lion, the marine iguana was able to maneuver in a heavy crashing surf. As I watched some in such situations, they appeared to be completely engulfed by churning currents of frothy water, disappearing, only to reappear in a few moments, bobbing at the surface. I saw them ride breaking waves onto the reef and quickly scamper up on the lava.

When resting on the surface of the sea, they often bob cork-like, the legs spread to the side for balance. I have seen them bloating themselves by gulping air, noticeably distending their trunk regions. Their ability to do this may provide the mechanism which permits them to buoy themselves at various depths when feeding.

When swimming, the iguana brings the front legs back along the side of the trunk and the hind legs back alongside the base of the tail. It undulates the tail from side to side and is thus propelled forward. Its head is held alertly above the surface as it swims. To dive, it ducks the head beneath the surface and with a quick lash of the tail is submerged. Under water, it swims in the same undulating manner, though the head is held straight forward.

For many years attempts to maintain marine iguanas in captivity were unsuccessful. Recently however, zoos in the United States and Europe have successfully exhibited these lizards. David Wilson (personal communication) of the Zoological Park in Edinburgh, Scotland, kept a Hood Island iguana for five years (it injured itself on a heating pipe and succumbed soon after). The Chicago Zoological Park has four which had survived fourteen months as of July, 1965, (Pawley, 1965). An attempt to establish a population of marine iguanas on Bermuda in 1933 proved unsuccessful (Wingate, 1965).

Summary

The ecology and behavior of the marine iguana are intimately and uniquely interwoven into an existence on lava reefs and shores and the cool waters fringing the Galápagos Islands.

Intimately, because this endemic lizard is limited to this narrow strip, existing between the dry interior of these islands and the harshness and dangers of the open sea.

Uniquely, because of the many ways, it has evolved to fit into this limited environment.

Its abundance gives striking evidence of its success. As a primary consumer, it derives its energy directly from the lush beds of alga species found from shallow mangrove lagoons to the greater depths in open sea.

Morphologically it is adapted to this amphibious way of life. Dark, rough-scaled, and long-clawed, it is well camouflaged on the black lava and protected

from the rough abrasive surface over which it moves with ease up steep cliffs and down deep crevices. In the shallow waters or crashing surf, it clings easily to the lava, with little chance of it being dashed or washed away. It swims with agility, propelled by a laterally compressed tail, and is able to dive to depths up to 35 feet, freely moving about and buoying itself at these levels. Its short snout and laterally flattened triserrate teeth enable it to either rasp off short reef algae or to browse on the lusher growth at greater depths. The dangerous intake of salt water while feeding has been met by the efficient use of the salt-extracting gland.

The behavior patterns of the marine iguana in most ways are basically characteristic of the family Iguanidae, to which it belongs. Some features of its behavior, however, are specifically related to its peculiar marine-amphibious existence.

Behavioral characteristics shared with other iguanids include its territorial defense, aggressive display involving a species-specific display-action-pattern, rapid nodding of the head during courtship, the hold on the female taken by the male during copulation, and the digging of a burrow in which to lay its eggs.

Special behavioral adaptations which have evolved and which are more or less peculiar to this species, are related to the stresses and particular features of its ecological niche.

Though the males are territorial for a part of each year, such aggressiveness appears to quickly break down once its function has been assured — the insemination of the females. This enables the males to again assemble in often large aggregations with little intermale antagonism and contributes to the conservation of energy. The stress of crowded territories is quickly ended.

The largest aggregations are associated with areas of islands which have adequate nesting localities such as sand beaches or areas of sufficient soil nearby. The limited availability of such nesting sites has probably contributed to the gregarious habits of this iguana and in particular to its communal nesting, a degree of gregarious nesting unknown for other lizards of any type.

As male territorial aggressiveness wanes, the now inseminated females are charged with completing the process of reproduction. They move from the wide reef areas and form aggregations near the nesting areas. Within these aggregations interfemale aggressiveness is evident as the females display at one another. Stimulated by each other, they move, first a few at a time, then in greater numbers, onto the beaches and begin to dig nest burrows. Here their aggressiveness reaches its peak as they squabble at the burrows, displaying, fighting, biting, head-butting, and riding, using the same aggressive gestures demonstrated by the males when holding territories. Though other female iguanids do display and show territorial tendencies, in the female marine iguana such behavior is limited to the time of nesting and the area of the nesting beach, when aggregations of females are involved.

The head-butting is known only in the marine iguana, and the enlarged conical scales capping the cranium of this lizard are probably an adaptation for such encounters.

The temperatures at which the marine iguana feeds are lower than those ambient temperatures encountered when out of water. Most iguanids feed during their peak activity, when their body temperatures are highest. The metabolic implications of these temperature relationships in the marine iguana need further investigation.

The breeding seasons of the marine iguana populations of the western islands of the archipelago are not synchronized with that of the marine iguanas of Hood Island, the island to the southeast of the entire group. There is nothing much different about this island when compared to the others except that it is the only known breeding site for the waved albatross. There are two possible, but speculative, explanations for this asynchrony in breeding seasons, with no good evidence to support either.

It may be that when extensive climatological data become available, such information will indicate a later wet season on Hood Island, which could influence the breeding season. It is also possible the western populations breed earlier to avoid the season of the garúa, the season of cool mists which hang over the islands. If the garúa does not effect Hood Island, this might help explain such a difference.

I do not know if a nestling waved albatross eats newly emerged marine iguanas or not, and I suspect it does not. But assuming that it would if available, this might be a possible explanation why the Hood Island iguanas breed later. A hatchling iguana, emerging from its nest in the area where a nestling albatross is alert and hungry might be quickly snapped up and devoured. If these hatchlings emerged after the albatrosses had fledged, then such danger would not occur. The albatross nesting begins in mid-April and it is probable that most fledging has taken place by the end of June. The marine iguanas on Hood Island probably lay their eggs in late March and April. Given a three-month or more incubation period, the hatchlings would emerge after the albatrosses had left the island.

The Hood Island race of the marine iguana is the most distinctive form of the species, indicating its longer isolation from the other populations. Perhaps its breeding season difference is a result of genetic drift, for the behavioral differences in the lava lizards (*Tropidurus*) of the Galápagos suggest such a possibility (Carpenter, 1962).

I believe that the Hood Island population is drifting away from the other populations in its display pattern, although the distinctions now are so slight as to defy proof from my data. I think further study will bear this out.

I have only been able to record the behavior of two large populations. There may be differences in other island populations also. On evidence offered by the

many examples of Galápagos interisland speciation (lava lizards, tortoises, snakes, finches, and numerous plants) such differences would be expected, and if not strongly evident now, may be apparent in a few hundred generations.

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